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Antoni STACHURSKI and Jerzy R. ZIMKA

Department of Biocenology, Institute of Ecology,
Polish Academy of Sciences, Dziekanów Leśny near Warsaw

# METHODS OF STUDYING FOREST ECOSYSTEMS: LEAF AREA, LEAF PRODUCTION AND WITHDRAWAL OF NUTRIENTS FROM LEAVES OF TREES*

ABSTRACT: Processes of withdrawal of elements (C and N) from leaves of trees in plant associations on soils variously provided with organic substances were examined. The withdrawal processes were found to depend on the type of soil and the tree species present. In ecosystems on soils poorly provided with organic substances (e.g., in *Pino-Quercetum*) the processes of withdrawal are more intensive than in richer systems (e.g., *Circaeo-Alnetum*). This is due to different withdrawal of C and N in the same species of trees growing on different soils and, to a greater extent, to the replacement of more strongly withdrawing species, e.g., hornbeam or pine, by weakly withdrawing species, e.g., alder.

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## 1. INTRODUCTION

Two general methods for calculating leaf production are known. The first method assumes that the biomass of green leaves, taken in the period of maximum biomass increase, is the total leaf production during the year. The second method assumes that leaf production is equal to their annual fall (M a d g w i c k 1970). Of course, both methods yield diminished values for production as they do not take into consideration losses of production due to consumption by phytophages, which in forest ecosystems are in general small, of the order of several per cent

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(Bray 1964, Kaczmarek 1967, Reichle and Crossley 1967). Another limitation of the method taking leaf fall as equal to production is that it does not consider losses in leaf production due to the processes of withdrawal and leaching of elements in autumn. The main aim of this work was to determine the extent of these losses and to compute more precisely leaf production taking these processes into consideration. At the same time as we had at our disposal data concerning general losses due to withdrawal and leaching we were able to measure these processes for some elements.

## 2. METHODICAL ASSUMPTIONS

Losses of leaf biomass due to withdrawal and leaching of elements may be determined directly by measuring on the trunk the leaf biomass per surface area unit and referring it to the total leaf fall biomass. The difference in biomass of these two parameters would be an indication of losses due to withdrawal and leaching. In the present work a much simpler and less cumbersome method was used. If green leaves of a given species are collected after termination of biomass increase, then the increase in surface area until the end of the vegetative season will be 0. In a situation when the leaf surface area does not change any changes in leaf mass of a determined surface area unit of green and falling leaves in autumn can only be due to withdrawal processes or to leaching of elements in the last stages of the vegetative season. Thus it is sufficient to compare the weight of a determined surface area of green leaves and fallen leaves (e.g., 1 $cm^2$): the difference of these two measurements will be an indication of biomass loss due to withdrawal processes or leaching. Thie can be expressed by the following equation where the index of leaf biomass loss ($r$) will have the following form:

$$r = \frac{w_l}{w_d} \quad \text{or} \quad r = \frac{w_l - w_d}{w_l} \cdot 100 \tag{1}$$

where: $w_l$ is the weight of 1 $cm^2$ of green leaves, $w_d$ – weight of 1 $cm^2$ of fallen leaves. Therefore the leaf production ($P_l$) calculated on the basis of leaf fall and supplemented by a correction for withdrawal and leaching of elements has the following form:

$$P_l = F_l \cdot r \tag{2}$$

where $F_l$ is the annual sum of biomass of fallen leaves registered by leaf traps, $r$ – index of loss of leaf biomass caused by withdrawal or leaching [formula (1)]. Having at our disposal general losses of biomass per surface unit (the difference $P_l - F_l$) we may attempt to present the data for withdrawal and leaching of some elements in a quantitative fashion. The information concerning the general loss of biomass is necessary for this as it appears that the direct comparison of the per cent of a given element in green and fallen leaves is not conclusive. This can be illustrated by the following example. Theoretically the per cent content of a given element may be: (1) the same, (2) higher or (3) lower than in green leaves. In the first case the content of the element may be maintained at the same level in spite of the occurrence of withdrawal or leaching due to the fact that all elements are removed to the same extent. In the second case the per cent content of a given element may be higher in fallen leaves even though

it was withdrawn because other elements were withdrawn to a relatively higher degree. The third possibility, i.e., when the per cent content of a given element is higher in fallen than in green leaves, does not guarantee that this element has been withdrawn or leached. In the last part of the vegetative season accumulation of elements is frequently observed in plants, e.g., Ca which is returned to the soil by the plant in the leaf fall (Olsen 1948, Tamm 1951). Therefore this phenomenon may cause a decrease in the per cent content of other elements, which has the appearance of withdrawal or leaching.

The above-mentioned considerations seem to indicate that the direct comparison of the content of some element in green and fallen leaves not only does not create the possibility of a quantitative consideration of the discussed processes but also does not even create a quantitative basis for stating that these processes are taking place. Information on general loss of leaf biomass in the last stages of the vegetative season is thus necessary.

The processes of withdrawal and leaching ($R_l$) of a given element may be presented as follows:

$$R_l = (P_l \cdot e_{cf}) - (F_l \cdot e_{cd}) \tag{3}$$

where: $P_l$ is the symbol of production of leaves of a given tree species per surface unit in g or mg, $e_{cf}$ is the per cent content of a given element in green leaves taken after cessation of growth of leaf biomass, $F_l$ – biomass of leaf fall of a given tree species, $e_{cd}$ – per cent of a given element in fallen leaves.

In some cases, e.g., when a comparison is made between the withdrawal and leaching elements in the same species of tree in different ecosystems it is easier to use the per cent form:

$$R_l = \frac{(P_l \cdot e_{cf}) - (F_l \cdot e_{cd})}{P_l \cdot e_{cf}} \cdot 100 \tag{4}$$

The symbols are the same as in equation (3).

If information on such parameters as the weight of a unit of surface, e.g., 1 $cm^2$ of green leaves is available and on leaf fall it is easy to compute the total assimilatory surface of a given species of tree. These calculations may be made on the basis of the following formula:

$$L_a = \frac{P_l}{w_d} \quad \text{or} \quad L_a = \frac{F_l}{w_l} \tag{5}$$

where: $w_d$ and $w_l$ indicate respectively the weight of 1 $cm^2$ of fallen leaves or green leaves of a given tree species. The symbols $F_l$ and $P_l$ are used in the same sense as above.

## 3. AREA AND METHODS

In the present work material collected in six forest associations of the Kampinos National Park was used: *Vaccinio myrtilli-Pinetum* (Kobendza, 1930), *Pino-Quercetum* (Kozłowska, 1926), *Circaeo-Alnetum* (Oberd., 1953), *Carici elongatae-Alnetum* (Koch, 1926) and in two

associations of *Tilio-Carpinetum* (Traczyk, 1962). One of the two is located on a large area neighbouring with *Pino-Quercetum* and the other is a small island within *Carici elongatae-Alnetum*.

In 1973 green leaves of deciduous trees were collected during the usual period of their maximal biomass, i.e., at the end of July. The leaves of conifers were collected during the period of vegetative rest of the pine tree – at the end of October. Only 2 and 3 year old needles were used for the analyses.

The end of October was also the period when fallen leaves were collected both for deciduous trees and conifers. According to previously obtained data this period is characterised by the greatest intensity of leaf fall.

The soil for chemical analysis was taken once (20 samples in each habitat) in mid-June, 1973. Both plant and soil material were dried until a constant weight at about 65°C.

The weight of 1 $cm^2$ of green or fallen leaves was obtained by cutting circles 1.65 $cm^2$ in area. As it is very difficult to calculate the weight of a given surface unit for pine needles the collected pine needles (green and fallen ones) were divided into 4 classes of length: 6.0–6.5 cm, 6.5–7.0 cm, 7.0–7.5 cm and 7.5–8.0 cm. This made it possible to compare the mass of green and fallen needles of the same length.

Chemical analyses of organic C and N were performed on a gas chromatograph CHN produced by Carlo Erba mod. 1102. Each measurement of a given plant or soil fraction was repeated 10 times.

## 4. RESULTS

The examined associations were divided into two groups of habitats: with low and high content of organic matter in the soil. Among the associations with low content of organic substances were: *Vaccinio myrtilli-Pinetum* (N = 0.10%, C = 0.77%), *Pino-Quercetum* (N = 0.08%, C = 0.26%) and the *Tilio-Carpinetum association located next to Pino-Quercetum* (N = 0.17%, C = 1.95%). *Circaeo-Alnetum* (N = 0.90%, C = 11.38%), the second *Tilio-Carpinetum* association located within *Carici elongatae-Alnetum* (N = 0.42%, C = 5.77%) and *Carici elongatae-Alnetum* (no soil samples were taken but this association was

Tab. I. Per cent of weight loss of fallen as compared with green needles of the pine (*Pinus silvestris* L.) in habitats poor and rich in organic substances

| Habitats | Per cent of N and C in the soil (at level $A_2$) | | Total number of analysed needles | Weight of one needle (mg) | | Per cent of weight loss of fallen as compared with green needles | Calculation coefficient (*r*) |
|---|---|---|---|---|---|---|---|
| | N | C | | green | fallen | | |
| Poor in organic substances | 0.12 | 1.11 | 295 | 23.62 | 16.18* | –28.8 | 1.40 |
| Rich in organic substances | 0.66 | 8.57 | 191 | 20.05 | 19.58** | –2.3 | 1.04 |

*Significance of differences at the 0.01 level.
**Significance of differences above the 0.01 level.

included among those with soils rich in organic matter on the basis of its thick humus layer) were included among habitats with soil rich in organic matter. The two types of habitats differ considerably in the content of organic matter. The differences are almost 6-fold in the case of nitrogen and are even bigger – about 8-fold – for carbon (Tabs. I–IV). Within each group the weight units of green and fallen leaves in the dominant types of trees were compared.

Tab. II. Per cent of weight loss of fallen as compared with green leaves of the hornbeam (*Carpinus betulus* L.) in habitats poor and rich in organic substances

| Habitats | Per cent of N and C in the soil (at level $A_2$) | | Total number of analysed leaf discs | Weight of 1 $cm^2$ of leaves (mg) | | Per cent of weight loss of fallen as compared with green leaves | Calculation coefficient (r) |
|---|---|---|---|---|---|---|---|
| | N | C | | green | fallen | | |
| Poor in organic substances | 0.12 | 1.11 | 300 | 4.98 | 3.16* | –36.5 | 1.58 |
| Rich in organic substances | 0.66 | 8.57 | 189 | 4.38 | 4.21** | –3.8 | 1.04 |

*Significance of differences at the 0.01 level.
**Significance of differences above the 0.01 level.

Tab. III. Per cent of weight loss of fallen as compared with green leaves in the oak (*Quercus robur* L.) in habitats poor and rich in organic substances

| Habitats | Per cent of N and C in the soil (at level $A_2$) | | Total number of analysed leaf discs | Weight of 1 $cm^2$ of leaves (mg) | | Per cent of weight loss of fallen as compared with green leaves | Calculation coefficient (r) |
|---|---|---|---|---|---|---|---|
| | N | C | | green | fallen | | |
| Poor in organic substances | 0.12 | 1.11 | 316 | 5.61 | 4.63* | –17.4 | 1.21 |
| Rich in organic substances | 0.66 | 8.57 | 411 | 5.66 | 5.48** | –3.1 | 1.04 |

*Significance of differences at the 0.01 level.
**Significance of differences above the 0.01 level.

Tab. IV. Per cent of weight loss of fallen as compared with green leaves in the alder (*Alnus glutinosa* L.) in habitats rich in organic substances

| Per cent of N and C in the soil (at level $A_2$) | | Total number of analysed leaf discs | Weight of 1 $cm^2$ of leaves (mg) | | Per cent of weight loss of fallen as compared with green leaves | Calculation coefficient (r) |
|---|---|---|---|---|---|---|
| N | C | | green | fallen | | |
| 0.66 | 8.57 | 248 | 5.94 | 6.87* | +15.6 | 0.87 |

*Significance of differences at the 0.01 level.

In habitats poor in organic substances the loss of weight of fallen as compared with green leaves is considerable. In the pine these differences are about 29%, in the hornbeam even 36%, and are the lowest in the oak – 17%. These phenomena are completely different in habitats with soil rich in organic substances. The per cent differences in weight between green and fallen leaves are small – 2%, approx. 4% and approx. 3% for the pine, hornbeam and oak, respectively. These differences are statistically significant at the 0.01 level (Tabs. I–III). In the alder the weight of 1 $cm^2$ of fallen leaves is even 15% higher than that of green leaves (Tab. IV) with the difference significant at the 0.01 level.

The processes of withdrawal and leaching of elements in trees growing in habitats which are rich in organic substances are thus completely different than in poor ones. They are intensive in habitats poor in organic substances and small or absent (e.g., the alder) in rich habitats. It seems that most of the loss in weight of fallen leaves is due to withdrawal of elements to trunks and roots rather than to leaching. The fact that there are differences in different habitats would be an indication of this as leaching should be similar in both rich and poor habitats.

The differentiation of withdrawal of elements in particular habitats affects the precision of calculation of leaf production. This can be illustrated by results presented in Table V, in which leaf production calculated on the basis of the yearly sum of leaf fall of a given tree without and with taking into consideration withdrawal of elements are compared. In an association with a low content of organic substances in the soil, *Pino-Quercetum*, the yearly sum of fallen leaves of 3 dominant species is much lower than in the association *Circaeo-Alnetum* which is characterized by a high content of organic substances. After taking into consideration withdrawal of elements the production of leaves in the two associations is found to be at similar level. Lower values of leaf production than leaf fall in the association *Circaeo-Alnetum* are due to the fact that in the alder, as was stated above, processes of returning elements dominate over their withdrawal.

Tab. V. An example of calculating leaf production for dominant tree species in two forest associations

| Association | Leaf species | Leaf fall ($g/m^2$/year) | Calculation coefficient ($r$) | Leaf production ($g/m^2$/year) |
|---|---|---|---|---|
| *Pino-Quercetum* | alder | – | – | – |
| | hornbeam | 50.2 | 1.58 | 79.2 |
| | oak | 98.1 | 1.21 | 118.3 |
| | pine | 101.2 | 1.40 | 141.4 |
| | sum | 249.5 | | 338.9 |
| *Circaeo-Alnetum* | alder | 280.6 | 0.87 | 234.0 |
| | hornbeam | 76.1 | 1.04 | 79.0 |
| | oak | 42.6 | 1.04 | 44.3 |
| | pine | – | – | – |
| | sum | 399.3 | | 357.3 |

It seems that the facts presented here unequivocally indicate the necessity of introducing a correction for withdrawal of elements by trees in calculation of leaf production based on leaf fall. This is especially important if differentiated associations with various types of soils and tree species are considered.

The phenomena of element withdrawal were observed in detail for carbon and nitrogen in two associations: *Pino-Quercetum* and *Circaeo-Alnetum*. Even cursory comparison of the per cent content of nitrogen in green and fallen leaves indicates that withdrawal of this element is possible. Fallen hornbeam leaves or pine needles have a much lower nitrogen content than green leaves and needles. In the same species the nitrogen content in fallen leaves is in general higher in *Circaeo-Alnetum* than in *Pino-Quercetum* (Tab. VI). According to the considerations in the methodical part of this work this may indicate different intensity of withdrawal of elements in the two associations. This is, however, not non-controversial proof. Applying calculations based on the differences in leaf production and leaf fall expressed in weight units of organic nitrogen we found that the analysed associations – *Pino-Quercetum* which has soil poor in organic substances and *Circaeo-Alnetum* – differ considerably in respect to the intensity of processes of nitrogen withdrawal. In the association *Pino-Quercetum* all the dominant tree species withdraw considerable quantities of nitrogen: the hornbeam approx. 64%, the oak approx. 63% and the pine as much as 77% which gives a summary withdrawal of 70%. In the association *Circaeo-Alnetum* both the hornbeam and the oak withdraw considerably less nitrogen (37% and 45%, respectively). Moreover, the main dominant species in this habitat, the alder, has the lowest withdrawal of nitrogen – only 5%. This gives 14% as the net nitrogen withdrawal for this association (Tab. VI). The mechanism of different withdrawal of nitrogen in the associations *Pino-Quercetum* and *Circaeo-Alnetum* is of two types: first, there are differences between the same species in the two associations and, secondly, the structure of the associations is different and the alder which withdraws the smallest amounts of nitrogen replaces the pine which withdraws the greatest amounts.

These phenomena are similar in the case of carbon withdrawal. In the association *Pino-Quercetum* all dominant tree species withdraw considerable amounts of this element. In the association *Circaeo-Alnetum* these values are lower. The pine is replaced by the alder in this association and the latter species even returns carbon with the fallen leaves in the amount approx. 21%. Therefore the net processes of withdrawal in *Pino-Quercetum* dominate – about 28% C is withdrawn, and in *Circaeo-Alnetum* return processes dominate – more carbon (by 11%) is returned to the soil with falling leaves than is found in the summer in live green leaves (Tab. VII).

The withdrawal of both analysed elements in the associations *Pino-Quercetum* and *Circaeo-Alnetum* have thus different values, which may indicate different regulation of distribution of these elements.

The method used also gave the possibility of computing the leaf area of tree leaves. As we had no simple method for calculating leaf area in conifers we only compared the associations *Circaeo-Alnetum* and *Carici elongatae-Alnetum* in which the pine occurs only sporadically. The total leaf area of all species of trees and shrubs is about 7.4 $m^2/m^2$ in *Circaeo-Alnetum* and is slightly higher than that in *Carici elongatae-Alnetum* – about 6.1 $m^2/m^2$ (Tab. VIII). The differences in leaf fall in the two associations are similar. Therefore it seems that in the case of deciduous trees leaf fall may be treated as an exponent of the leaf area which is in agreement with the postulates of S a t o o (1970).

## 5. DISCUSSION

One of the debatable questions is the manner of calculating the total primary production of trees which is composed of leaf and woody material production (branches, trunks and roots). The withdrawal of elements and the decrease in production of leaves calculated by the fall

Tab. VI. Comparison of the withdrawal of nitrogen in dominant species in two forest associations

| Association | Leaf species | Per cent of N content in leaves | | Leaf production | Leaf fall | Leaf production | Leaf fall | Withdrawal of element | |
|---|---|---|---|---|---|---|---|---|---|
| | | green | fallen | $g/m^2$/year | | g $N/m^2$/year | | g $N/m^2$/year | per cent |
| *Pino-Quercetum* | alder | – | – | – | – | – | – | – | – |
| | hornbeam | 1.98 | 1.11 | 79.2 | 50.2 | 1.57 | 0.56 | –1.01 | –64.33 |
| | oak | 2.24 | 1.01 | 118.3 | 98.1 | 2.65 | 0.99 | –1.66 | –62.64 |
| | pine | 1.64 | 0.53 | 141.4 | 101.2 | 2.32 | 0.54 | –1.78 | –76.72 |
| | sum | – | – | 338.9 | 249.5 | 6.54 | 2.09 | –4.45 | –68.04 |
| *Circaeo-Alnetum* | alder | 3.53 | 2.81 | 234.0 | 280.6 | 8.26 | 7.88 | –0.38 | –4.60 |
| | hornbeam | 2.23 | 1.46 | 79.0 | 76.1 | 1.76 | 1.11 | –0.65 | –36.93 |
| | oak | 2.58 | 1.49 | 44.3 | 42.6 | 1.14 | 0.63 | –0.51 | –44.73 |
| | pine | – | – | – | – | – | – | – | – |
| | sum | – | – | 357.3 | 399.3 | 11.16 | 9.62 | –1.54 | –13.79 |

Tab. VII. Comparison of the withdrawal of carbon in dominant tree species in two forest associations

| Association | Leaf species | Per cent of C content in leaves | | Leaf production | Leaf fall | Leaf production | Leaf fall | Withdrawal of element | |
|---|---|---|---|---|---|---|---|---|---|
| | | green | fallen | $g/m^2/year$ | | $g\ C/m^2/year$ | | $g\ C/m^2/year$ | per cent |
| *Pino-Quercetum* | alder | – | – | – | – | – | – | – | – |
| | hornbeam | 47.27 | 45.96 | 79.2 | 50.2 | 37.44 | 23.07 | –14.37 | –38.38 |
| | oak | 47.66 | 46.17 | 118.3 | 98.1 | 56.38 | 45.29 | –11.09 | –19.67 |
| | pine | 51.26 | 50.55 | 141.4 | 101.2 | 72.48 | 51.16 | –21.32 | –29.41 |
| | sum | – | – | 338.9 | 249.5 | 166.30 | 119.52 | –46.78 | –28.12 |
| *Circaeo-Alnetum* | alder | 47.95 | 48.33 | 234.0 | 280.6 | 112.20 | 135.61 | +23.41 | +20.86 |
| | hornbeam | 47.24 | 44.85 | 79.0 | 76.1 | 37.32 | 34.13 | –3.19 | –8.54 |
| | oak | 46.29 | 46.04 | 44.3 | 42.6 | 20.51 | 19.61 | –0.90 | –4.38 |
| | pine | – | – | – | – | – | – | – | – |
| | sum | – | – | 357.3 | 399.3 | 170.03 | 189.35 | +19.32 | +11.36 |

Tab. VIII. Calculation of leaf area for deciduous tree species in two forest associations

| Association | Leaf species | Leaf fall ($g/m^2$/year) | Weight of 1 $cm^2$ of fallen leaves (mg) | Leaf area ($m^2/m^2$) |
|---|---|---|---|---|
| *Circaeo-Alnetum* | alder | 280.6 | 6.87 | 4.08 |
| | hornbeam | 76.1 | 5.16 | 1.81 |
| | oak | 42.6 | 5.31 | 0.78 |
| | birch | 11.6 | 5.80 | 0.20 |
| | linden | 5.3 | 2.29 | 0.23 |
| | hazel | 8.9 | 3.63 | 0.22 |
| | alder buckthorn | 2.0 | 3.15 | 0.06 |
| | sum | 427.1 | – | 7.38 |
| *Carici elongatae-Alnetum* | alder | 322.6 | 5.62 | 5.74 |
| | hornbeam | – | – | – |
| | oak | 2.9 | 6.03 | 0.05 |
| | birch | 6.6 | 5.36 | 0.12 |
| | linden | – | – | – |
| | hazel | 1.0 | 3.62 | 0.03 |
| | alder buckthorn | 3.8 | 2.80 | 0.14 |
| | sum | 336.9 | – | 6.08 |

method are possible to avoid. The leaf fall may be added to the annual increases of the trunk and branches as was done by Duvigneaud and Denaeyer-De Smet (1970).

If we are not interested in the quantitative aspects of withdrawal of elements this method also seems less tedious due to the fact found in the present work that leaf fall may sometimes (for some associations) reach slightly higher values than leaf production in the summer maximum of their mass. This makes the matter more complicated as it is not possible to say whether net leaf production is the result of photosynthesis (the amount of carbon increases) or an effect of translocations of some elements from the trunk related with preparations for the vegetative period.

A more precise value for green mass production may be obtained if phytophage consumption is calculated, especially in the cases in which it reaches a considerable value (materials on this problem are in preparation).

Regardless of the methodical aspect the obtained results appear to concern essential ecological problems. The differentiation of withdrawal of elements in ecosystems is decisive for the abundance of fallen leaves in elements. On this depends mineralization, and on this in turn the food resources in the soil. The C/N ratio in falling material is especially important here (Reichle 1971).

In the case of the associations examined in this work different intensities of carbon and nitrogen withdrawal caused the litter C/N ratio to be 53.0 in *Pino-Quercetum*, and only 20.2 in *Circaeo-Alnetum*. The respective values of rate of litter decomposition were about 0.50 for *Pino-Quercetum* and about 1.18 for *Circaeo-Alnetum* (Stachurski and Zimka 1975). This indicates that the processes of element circulation are much faster in ecosystems with a lower C/N ratio. Taking into consideration the processes of element withdrawal as well as the

species structure of the plants seems to be essential for the precision of calculation production but also allows us to grasp an important factor affecting the rate of element circulation.

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## 6. SUMMARY

The paper describes the method of calculating losses in leaf mass due to the processes of element withdrawal by plants at the end of the vegetative season. This makes more precise evaluation of leaf production possible as well as the characterization of various forest ecosystems in respect to the intensity of element withdrawal. The investigations were performed on six forest associations of the Kampinos National Park: *Vaccinio myrtilli-Pinetum*, *Pino-Quercetum*, two *Tilio-Carpinetum* associations, *Circaeo-Alnetum* and *Carici elongatae-Alnetum*.

The analysed plant ecosystems had different degrees of soil abundance in organic substances. The range was 0.62–11.38% C. The following facts were demonstrated:

1. The weight losses of falling as compared to green leaves reflect the processes of withdrawal of many elements from the leaves and depend on the species of tree and on the type of soil on which it is growing. In ecosystems of soils with low organic content (e.g., *Pino-Quercetum*) the intensity of withdrawal processes is high – in the range 17–36%, depending on the tree species. In ecosystems with soil rich in organic substances (e.g. *Circaeo-Alnetum*) these processes attain the intensity of only a few per cent (pine – 2.4%, oak – 3.0%, hornbeam – 4.0%). In the alder, which is dominant in such rich habitats, these processes are null or in some cases elements are added to fallen leaves (Tabs. I–IV).

2. The greater intensity of withdrawal processes in plants from ecosystems with soil poor in organic matter leads to considerable underestimations of production of leaves evaluated by the fall method. After taking into consideration the correction for weight loss in fallen leaves the leaf production in ecosystems which appear to differ is in fact similar (Tab. V).

3. Particular elements are selectively withdrawn from leaves – e.g., nitrogen is withdrawn by 26–48% more than carbon. Ecosystems with soil poor and rich in organic matter were found to differ in the extent of withdrawal of these elements from leaves. In ecosystems poor in organic matter the withdrawal processes are much more intensive than in rich habitats. This rule is realized by two methods. First, the same species withdraw less C and N in richer ecosystems. Secondly, the species structure of the associations changes and species which strongly withdraw elements such as the pine or the hornbeam are replaced by a poorly withdrawing species – the alder (Tabs. VI, VII).

4. The comparison of the weight of fallen leaves with the leaf area indicates that in ecosystems with uniquely deciduous trees the leaf fall is proportional to the leaf area and therefore may be considered as an index (Tab. VIII) of leaf area.

## 7. POLISH SUMMARY (STRESZCZENIE)

W pracy opisano metodykę obliczania strat ciężaru listowia, wywołanych procesami wycofywania pierwiastków przez rośliny pod koniec sezonu wegetacyjnego. Umożliwiło to bardziej precyzyjną ocenę produkcji liści oraz charakterystyki różnych zespołów leśnych pod kątem nasilenia procesów wycofywania pierwiastków. Badania przeprowadzono w sześciu zespołach leśnych Kampinoskiego Parku Narodowego: *Vaccinio myrtilli-Pinetum*, *Pino-Quercetum*, w dwu zespołach *Tilio-Carpinetum*, *Ciracaeo-Alnetum* i *Carici elongatae-Alnetum*.

Analizowane zespoły roślinne charakteryzowały się różną zasobnością gleb w substancje organiczne. Zakres zmienności zawierał się w granicach 0.62–11.38% C. W oparciu o zastosowaną metodykę wykazano następujące fakty:

1. Straty ciężaru liści opadających w stosunku do zielonych, będące odzwierciedleniem procesów wycofywania wielu pierwiastków z listowia, są uzależnione od typu gleb i gatunków drzew na nich rosnących. W ekosystemach, których gleby charakteryzują się niską zawartością substancji organicznych (np. *Pino-Quercetum*), nasilenie procesów wycofywania u roślin jest wysokie – zawierające się w granicach 17–36%, zależnie od gatunku drzewa. Natomiast w ekosystemach o glebie bogatej w substancje organiczne (np.

*Circaeo-Alnetum*) procesy te osiagają nasilenie zaledwie rzędu kilku procent (np. u sosny – 2.4%, dębu – 3.0%, grabu – 4.0%). W przypadku olchy, gatunku dominującego w tak zasobnych środowiskach, procesy te mają wartości zerowe, a w niektórych przypadkach występuje nawet dodawanie pierwiastków w liściach opadających (tab. I–IV).

2. Większe nasilenie procesów wycofywania pierwiastków u roślin, w ekosystemach o glebach ubogich w substancje organiczne, powoduje znaczne niedocenianie produkcji liści, ocenianej metodą „opadową". Po uwzględnieniu poprawki na straty wagowe liści spadających, wynikające z wycofywania pierwiastków, okazało się, że produkcja liści w ekosystemach pozornie różniących się pod tym względem jest zbliżona (tab. V).

3. Poszczególne pierwiastki wycofywane są z liści selektywnie, np. azot jest wycofywany w około 26–48% większym stopniu niż węgiel. Stwierdzono przy tym, że ekosystemy o glebach ubogich i bogatych w organiczny azot i węgiel charakteryzują się odmiennym nasileniem wycofywania tych pierwiastków z listowia. W ekosystemach ubogich w substancje organiczne w glebie procesy wycofywania u roślin są znacznie intensywniejsze niż w bogatych. Prawidłowość ta realizuje się dwiema drogami. Po pierwsze, gatunki drzew powtarzających się we wszystkich ekosystemach wycofują z listowia coraz mniejsze ilości C i N. Po drugie, występuje zmiana struktury gatunkowej zespołu roślin: miejsce gatunków silnie wycofujących pierwiastki, np. grabu czy sosny, zajmuje gatunek słabo wycofujący – olcha (tab. VI, VII).

4. Porównanie ciężaru opadu liści z ich powierzchnią wskazuje, że w ekosystemach o wyłączności drzew liściastych ciężar liści opadłych jest proporcjonalny do powierzchni liści, w związku z czym może być traktowany jako jej wskaźnik (tab. VIII).

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Paper prepared by H. Dominas

AUTHORS' ADDRESS:
Dr Antoni Stachurski
Dr Jerzy R. Zimka
Zakład Biocenologii
Instytutu Ekologii PAN
Dziekanów Leśny k. Warszawy
05–150 Łomianki
Poland.